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ASTROHIPPIUS AND THE ORIGIN OF BLANCAN AND PLEISTOCENE HORSES

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Several years ago, I wrote a short paper (Dalquest, 1978) summarizing my thoughts concerning the phylogeny of American Blancan and Pleistocene horses. I suggested that the Blancan zebras (*Equus simplicidens* Cope and related species) were derived from late Hemphillian Land Mammal Age species of *Dinohippus* Quinn and that the Blancan ass, *Asinus cumminsii* (Cope), was descendent from a late Hemphillian species of the genus *Astrohippus* Stirton. The basic enamel patterns of the lower molar teeth are similar in the two genera but differ in all instances in the nature of the ectoflexid (Figs. 1-3). In the lower molars (not premolars) of *Dinohippus*, the ectoflexid usually is broad and blunt-ended, and always penetrates deeply into the molar isthmus. In *Astrohippus*, usually it is shorter, more slender and pointed, and never penetrates deeply into the molar isthmus. The Blancan zebras always have ectoflexids of the *Dinohippus*-type. Blancan asses always seem to have ectoflexids of the *Astrohippus*-type. The nature of the ectoflexids in zebras and asses is not an original observation; it was described in detail by Skinner *et al.* (1972). In practice (Fig. 1, right), one visualizes a line connecting the floors of the preflexid and postflexid (terminology of Skinner *et al.*, 1972; entoflexid and metaflexid of Quinn, 1955). In *Dinohippus* and the Blancan and Pleistocene zebras, the ectoflexid extends well past this line (Fig. 2); in *Astrohippus* and *Asinus*, the ectoflexid rarely reaches the line (Fig. 3). In some teeth with the preflexid and postflexid too

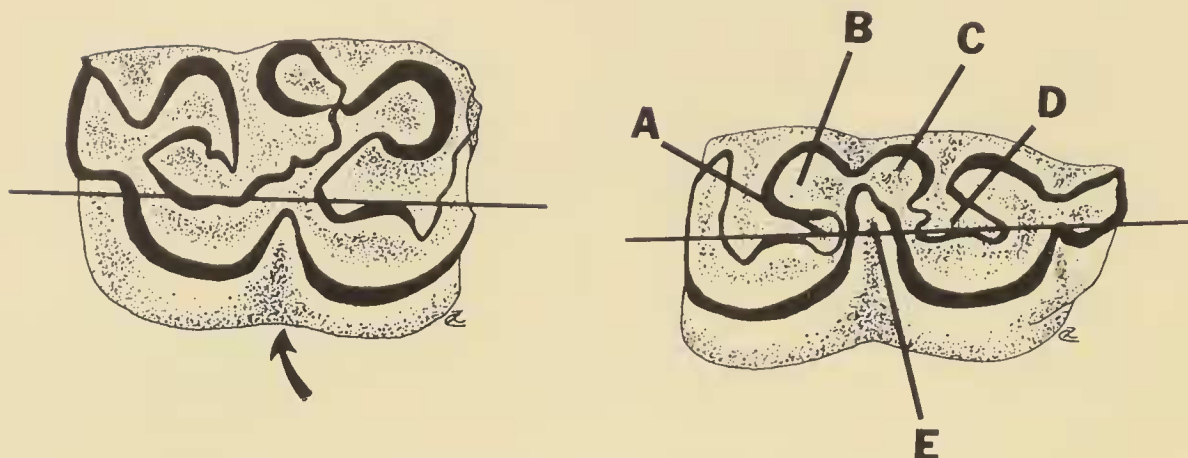


FIG. 1.—Left, lower third premolar of *Dinohippus interpolatus* (MWSU 7804, Coffee Ranch local fauna, mid-Hemphillian age) showing elongated molar isthmus and shallow ectoflexid typical of premolars in both the *Equus* and *Asinus* lineages. Right, lower second molar of *Dinohippus interpolatus* showing the structures important in separating the *Equus* and *Asinus* lineages: A, preflexid; B, metaconid; C, metastylid; D, postflexid; E, ectoflexid penetrating deeply into molar isthmus, well past line connecting floors of preflexid and postflexid.

twisted to establish a base line, it is still obvious whether the *Dinohippus* or *Astrohippus* type of ectoflexid is present. With advanced age, the ectoflexid in both genera tends to retreat from the isthmus, but the usually thick, often square-ended ectoflexid of the *Dinohippus*-type still penetrates the isthmus.

Described species of mid- to late-Hemphillian *Dinohippus* are large horses. These species are known from numerous local faunas, some having abundant fossil material. Contemporary species of *Astrohippus* are diminutive, their teeth easily separated from those of *Dinohippus* by their small size. Fossils of these taxa also are common in some local faunas, and more than 2000 teeth were examined in the course of this study. No *Dinohippus* molars with the *Astrohippus*-type ectoflexid were found, and none has been reported from elsewhere. Inasmuch as *Astrohippus* is similar to Blancan *Asinus* in such dental characters as size and configuration of the molar ectoflexid, it seems reasonable that a later species of *Astrohippus* should be the ancestor of Blancan asses rather than some hypothetical, unknown ancestor as has been maintained. No convincing proof that *Astrohippus* is not ancestral to *Asinus* ever has been offered.

My decision (1978) to place the Blancan zebras in a genus different from the asses was not based solely on the nature of the ectoflexid which separates them so completely. I believe *Equus* is descendent from *Dinohippus*, and *Asinus* from *Astrohippus*. To consider *Asinus* a subgenus of *Equus* when the two originated

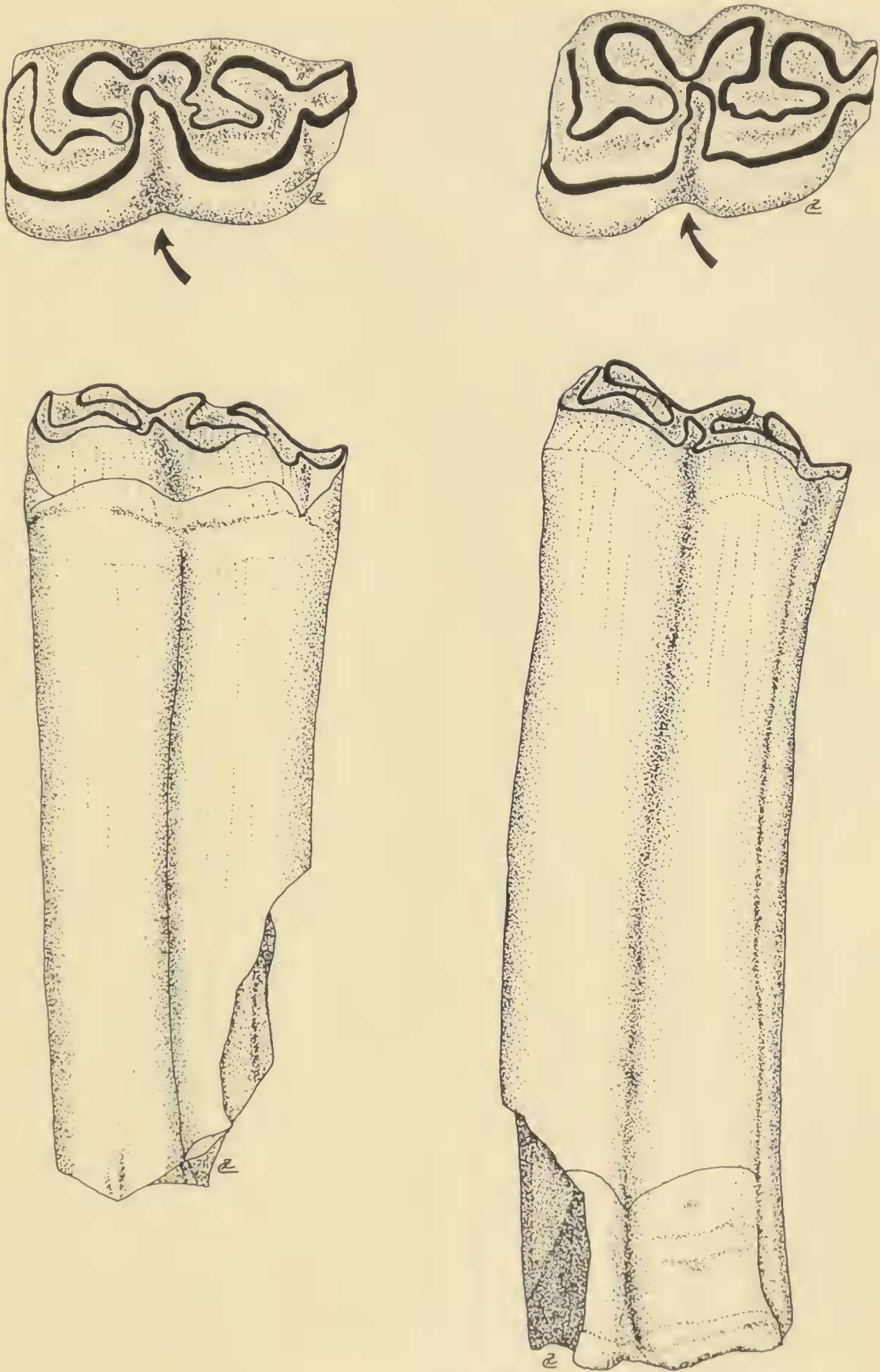


FIG. 2.—Ectoflexids of the *Dinohippus*-type. Left, lower second molar of *Dinohippus interpolatus* (MWSU 6256, Coffee Ranch local fauna, mid-Hemphillian age). Right, lower second molar of *Equus burchellii* (MWSU 1087, Recent, Mozambique).

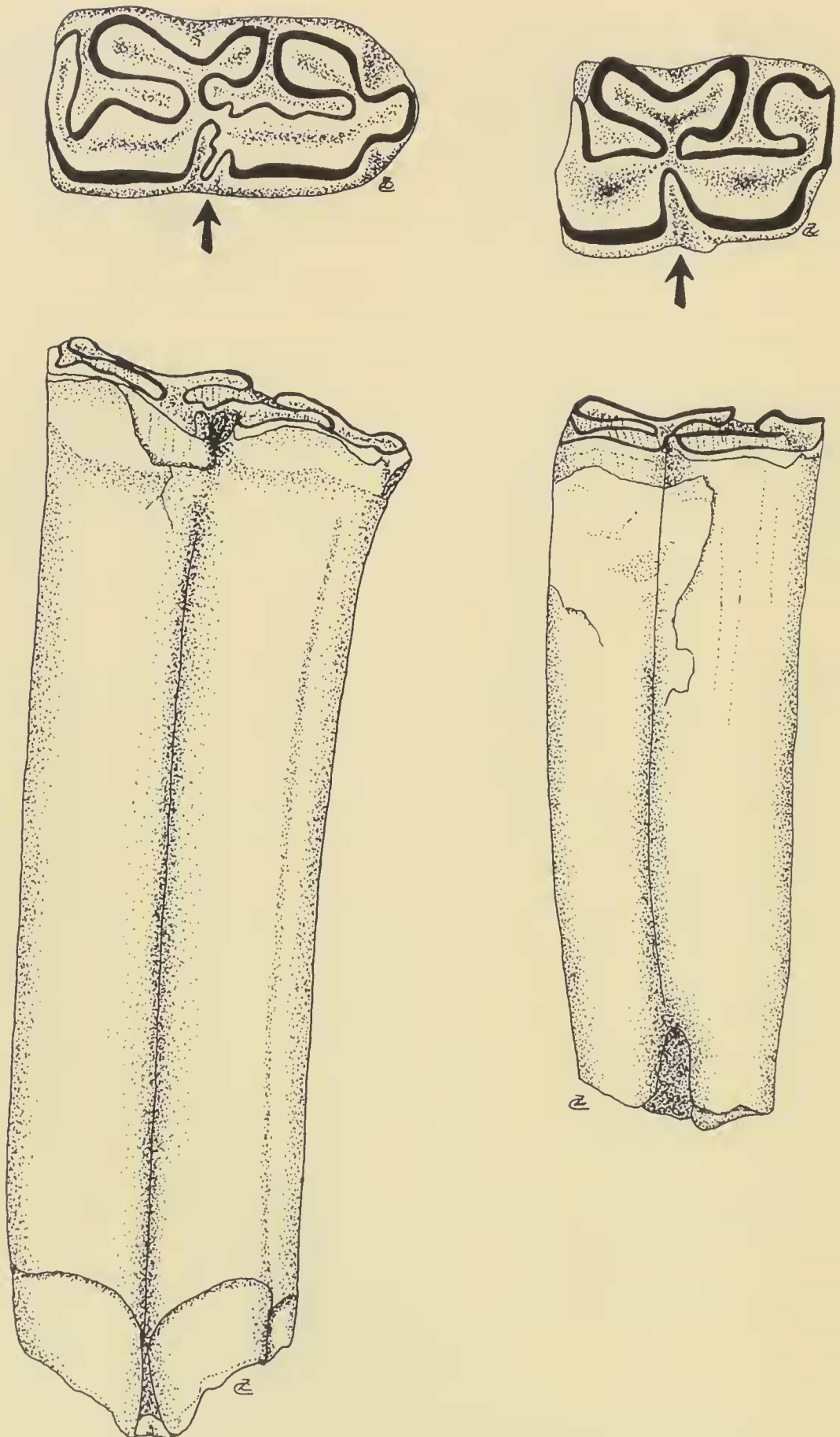


FIG. 3.—Ectoflexids of the *Astrohippus*-type. Left, lower second molar of *Asinus* cf. *excelsus* (MWSU 10648, late Pleistocene, Aguascalientes, México). Right, lower second molar of *Astrohippus albidens* (MWSU 11425-397, Ocote local fauna, late Hemphillian, México).

from different Hemphillian genera would imply an unacceptable level of convergence. Technically, this might be avoided by reducing *Dinohippus* and *Astrohippus* to subgenera of *Pliohippus* Marsh, but the diphyletic origin of *Equus* would remain. The *Equus* and *Asinus* lineages have been separated for more than six million years.

Some workers have disagreed with my conclusions. Bennett (1980) presented a cladistic analysis of some species of Pleistocene and modern horses. She considered *Asinus* to be a subgenus of *Equus*, limiting the genus *Equus* to include only *Equus* and *Asinus* as subgenera. Zebras, *Equus caballus* Linnaeus, and some species of Pleistocene horses were placed in *Equus* (*Equus*). Asses and some Pleistocene horse species were assigned to *Equus* (*Asinus*). Bennett denied the possibility of an origin of *Asinus* separate from that of *Equus*, postulating an unknown kind of *Dinohippus* as an ancestor. She thought that *Astrohippus* lacked a hypoconal groove in the upper molars (present in *Dinohippus*, *Equus*, and *Asinus*). However, all species of *Astrohippus* that I have seen have hypoconal grooves in the upper molars, although the groove may be absent in many individuals. This has long been documented; Stirton (1940) for example, when he established *Astrohippus* (as a subgenus of *Pliohippus*), figured a single molar of *Astrohippus ansae* (Matthew and Stirton). The tooth has a hypoconal groove typical of those of *Equus* and *Asinus*. The hypoconal groove is discussed in detail hereafter.

Bennett also considered the facial fossae to be an important character separating *Astrohippus* from *Asinus*, presuming that *Dinohippus* lacked facial fossae (present in *Astrohippus*) other than "an indentation along the rostrum below and anterior to the orbit which is the remnant of a facial fossae." Most species of mid- to late-*Dinohippus* have facial fossae, sometimes strongly developed (Matthew and Stirton, 1930; Lance, 1950; MacFadden, 1984). Facial fossae in the *Equus* lineage seem to have been lost progressively through the Hemphillian Land Mammal Age but still were present in Blancan *Equus* (Gazin, 1936). Similar progressive loss may be presumed in *Asinus* but cannot be documented because skulls of Blancan asses have not been discovered.

MacFadden (1984) discussed the facial fossae of late Hemphillian *Dinohippus* and *Astrohippus* in detail, and proposed *Dinohippus mexicanus* (Lance) as a possible ancestor of "some segment of the *Equus* radiation," but thought that the

complicated facial fossae of the contemporary *Astrohippus stocki* (Lance) prevented it from being ancestral to asses. I would argue that *Asinus cumminsii* might have descended from a species of *Astrohippus* other than *A. stocki*—one that had less strongly developed facial fossae—and that the loss of facial fossae might have taken place at variable rates in the two lineages. The mid-Hemphillian *Dinohippus interpolatus* (Cope) had strongly developed facial fossae, whereas the contemporary *D. leidyanus* (Osborn) has less well-developed fossae. MacFadden (1984) suggested that for this reason alone *D. interpolatus* belongs in a genus other than *Dinohippus*, but if *D. interpolatus* is a *Dinohippus* in all characters other than facial fossae, the character is suspect. The amount of sexual, age, and individual variation of facial fossae in Hemphillian horses needs careful statistical analysis. However, facial fossae are present in Hemphillian and Blancan horses and apparently sometimes in modern zebrine horses (Forstén, 1986b).

Some European workers have found fault with the ectoflexid when they attempted to apply the character to Old World Villafranchian and Pleistocene horses. I restricted my 1978 paper to American horses because I was aware that lower jaws of the domestic horse, *Equus caballus*, showed both the *Dinohippus* and *Astrohippus*-type ectoflexids. Old World horses must have been derived from American ancestors, but it is now clear that the evolution of the Old World horses proceeded differently than it did in America, as is discussed in greater detail hereafter.

GENERA AND SUBGENERA

The most common current treatment places all living equids in the genus *Equus* but, for reasons stated, I use *Equus* and *Asinus* as full genera. Groves and Mazak (1967) used a three-part division of living horses: *Equus* for wild and domestic horses, *Asinus* for the asses and onagers, and *Hippotigris* Smith, for the zebras. Quinn (1957) placed the onagers in the separate genus *Onager* Brisson (invalid name). Almost every species of modern monodactyl horse has been placed in a separate genus at one time or another. Many of these names have, at times, been considered subgeneric. Names proposed as genera or subgenera for Pleistocene horses are too numerous to list here. Nominal genera and subgenera for Old World horses are at least as numerous as those for New World species. Detailed synonymy must await revision of the Pleistocene equids.

In the following accounts, I use general terms as follows: caballoid for all late Tertiary to modern horses; caballine for *Equus caballus* and related species; zebrine for Old and New World zebras, living and extinct; asinine for the asses; and hemione for the onagers. This is similar to the grouping used by Forstén (1986b) except for use of caballine (rather than caballoid for the true horses) and zebrine (rather than stenonid) for the zebras. I think the older term, zebrine, is more descriptive than stenonid.

Dental characters used hereafter include the shape of the protocone in the upper molars, development of hypoconal groove in upper molars, nature of the ectoflexid in lower molars, and linguaeflexid of lower molars. Premolars must be disregarded. Generic names in quotation marks are as used elsewhere and may not agree with usage here.

HEMPHILLIAN CABALLOID HORSES

By the middle to late Hemphillian, American horses included only the tridactyl hipparions and the monodactyl caballoids, *Dinohippus* and *Astrohippus*. Accounts of these genera that follow are based on material in the Midwestern State University Collection of Fossil Vertebrates: several fragmentary maxillaries, a number of more or less fragmentary lower jaws, and about 300 isolated cheekteeth of *Dinohippus interpolatus* from the Coffee Ranch local fauna, mid-Hemphillian, of Texas (ca. six million years BP—Dalquest, 1983); several lower jaws and about 300 isolated cheekteeth of *Dinohippus ocotensis* (Mooser) from the Ocote local fauna of Guanajuato, México (ca. five million years BP—May and Repenning, 1982); several upper and lower jaw fragments and approximately 50 isolated teeth of *Astrohippus ansae* from the Coffee Ranch; and a few lower jaw fragments and more than 2000 isolated cheekteeth of *Astrohippus albidens* Mooser, from Ocote. Less than half of the available teeth are too greatly worn, completely unworn, or too damaged for use. Specimens utilized are permanent teeth that retain at least half of their estimated original height, as only in the upper part of the teeth of hypsodont horses are the enamel patterns significant.

Miller and Carranza-Castadeña (1984) considered *Dinohippus ocotensis* and *Astrohippus albidens* to be synonyms of *Dinohippus mexicanus* and *Astrohippus stocki* of the Yepómera local fauna of Chihuahua. Neither of the Ocote species is strongly differentiated when compared with the Yepómera horses, and no

dental characters firmly separate the species. Nevertheless, the Ocote population of *Dinohippus* generally seems to have more elongated and angular protocones of the upper molars than does the Yepómera population, and the Ocote *Astrohippus* seem to have, on the average, upper molars with more elongated protocones and lower molars with more sharply V-shaped linguaflexids than do the Yepómera horses. These are progressive characters that suggest slightly younger age for the Ocote horses, and for that reason I prefer to keep them as valid species.

Detailed study of any cheektooth character in slightly to moderately worn molars of species of Hemphillian or younger horses shows a large amount of variation. There is almost always an average condition for any character, which represents the evolutionary level for that species. If the range of variation in a single character is considered, a normal curve results (rare extremes may have to be disregarded; for example, two teeth of *Dinohippus ocotensis* with the protocones isolated as in the hipparions). At one side of the curve are specimens showing the characters of more primitive, ancestral species, whereas at the other side are teeth exhibiting progressive features that become the norm in later species. Although an individual tooth may not be identifiable to species, series of specimens can be referred with some confidence. The following discussions concern the norm (bulk of the specimens).

Structures of premolars are variable and nondiagnostic. In premolars of both *Dinohippus* and *Astrohippus*, the molar isthmus is long, the metaconid-metastylid column (double knot of Forstén, 1986b) appearing as though on a pedestal (Fig. 1, left). The isthmus of p2 is long, that of p3 slightly shorter, and that of p4 shortest. In *Dinohippus*, the progressive decrease in length of the molar isthmus tends to continue into the molars but this is not always true. In *Astrohippus*, the change from gradual reduction in isthmus length in the premolars often is followed by abrupt change to a uniformly short molar isthmus.

In Hemphillian horses, the primitive condition of the protocones of the molars is a smoothly-rounded oval shape with the protoconal isthmus short and broad, usually a mere constriction, and the body of the protocone lying entirely posterior to the isthmus. Pleistocene and modern *Equus* show the derived condition: narrowed and often elongated isthmus, with protocone elongated and flattened, and part of the body of the protocone lying anterior to the isthmus (Figs. 4-5).

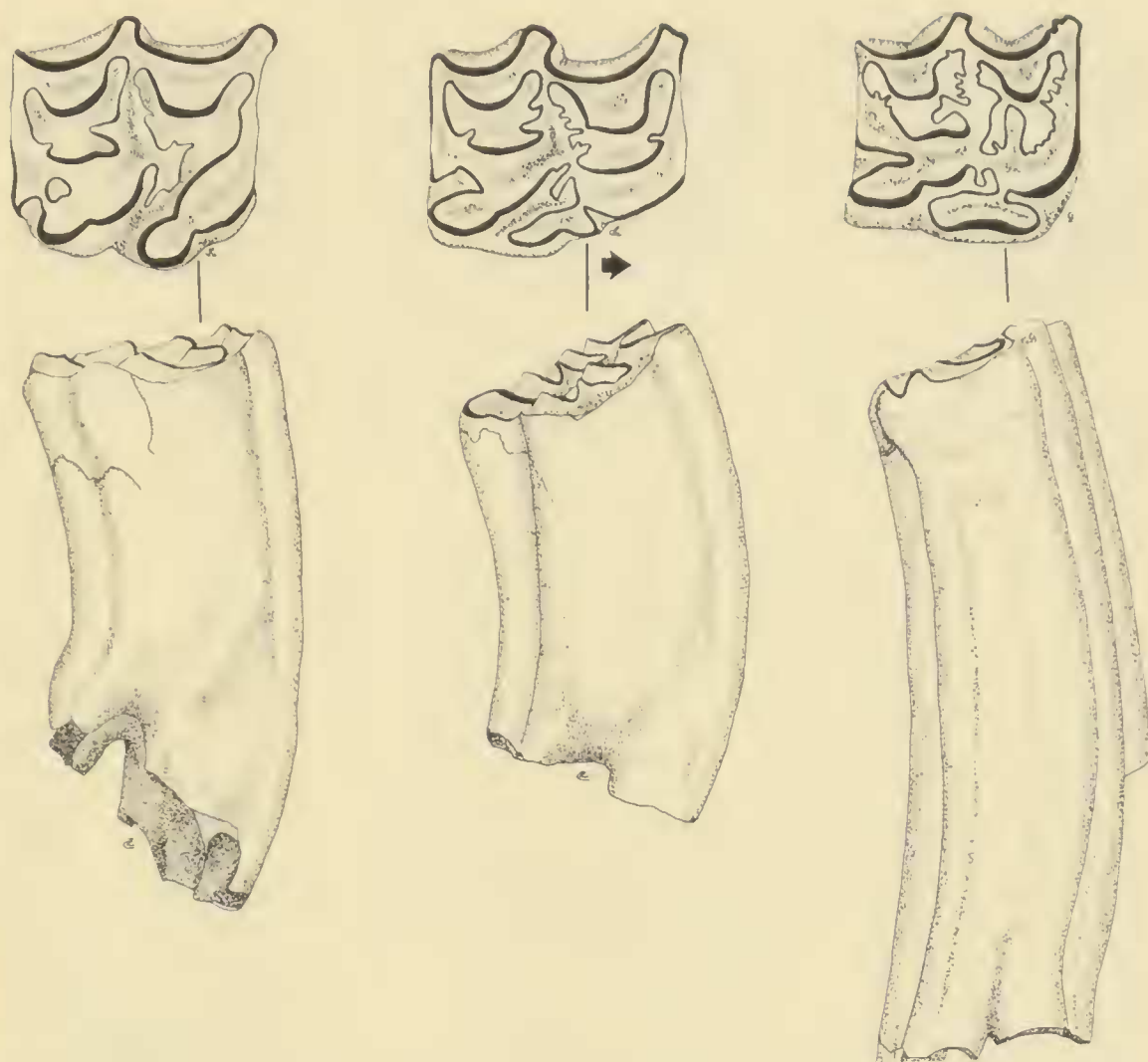


FIG. 4.—Progressive evolution of the protocone in the *Equus* lineage. Arrow indicates anterior. Left, primitive type with short isthmus, oval shape, and entire body of protocone posterior to anterior border of protoconal isthmus (MWSU 3998, first upper molar, Coffee Ranch local fauna); this type is not uncommon at the Coffee Ranch but, is rare at Ocote. Middle, grooved protocone, with a small part of the body extending anterior to the isthmus (MWSU 11623-192, second upper molar, Ocote local fauna); this is the common protocone type in the late Hemphillian Ocote local fauna. Right, advanced type with elongated isthmus, flattened, elongated body shape and much of the body extending anterior to the isthmus (MWSU 10192, first upper molar, late Pleistocene Cedazo local fauna, México); this is the common protoconal type in modern and Pleistocene *Equus* and *Asinus*.

Many teeth of mid-Hemphillian *Dinohippus interpolatus* and *Astrohippus ansae* have the protocone of primitive type. Advance is indicated in some teeth by flattening of the lingual wall in *Dinohippus* and development of grooves in the lingual wall in *Astrohippus*.

In the late Hemphillian, the protoconal isthmus of *Dinohippus ocotensis* remains short but the oval shape is largely lost. The enamel wall of the isthmus continues in a straight line to form

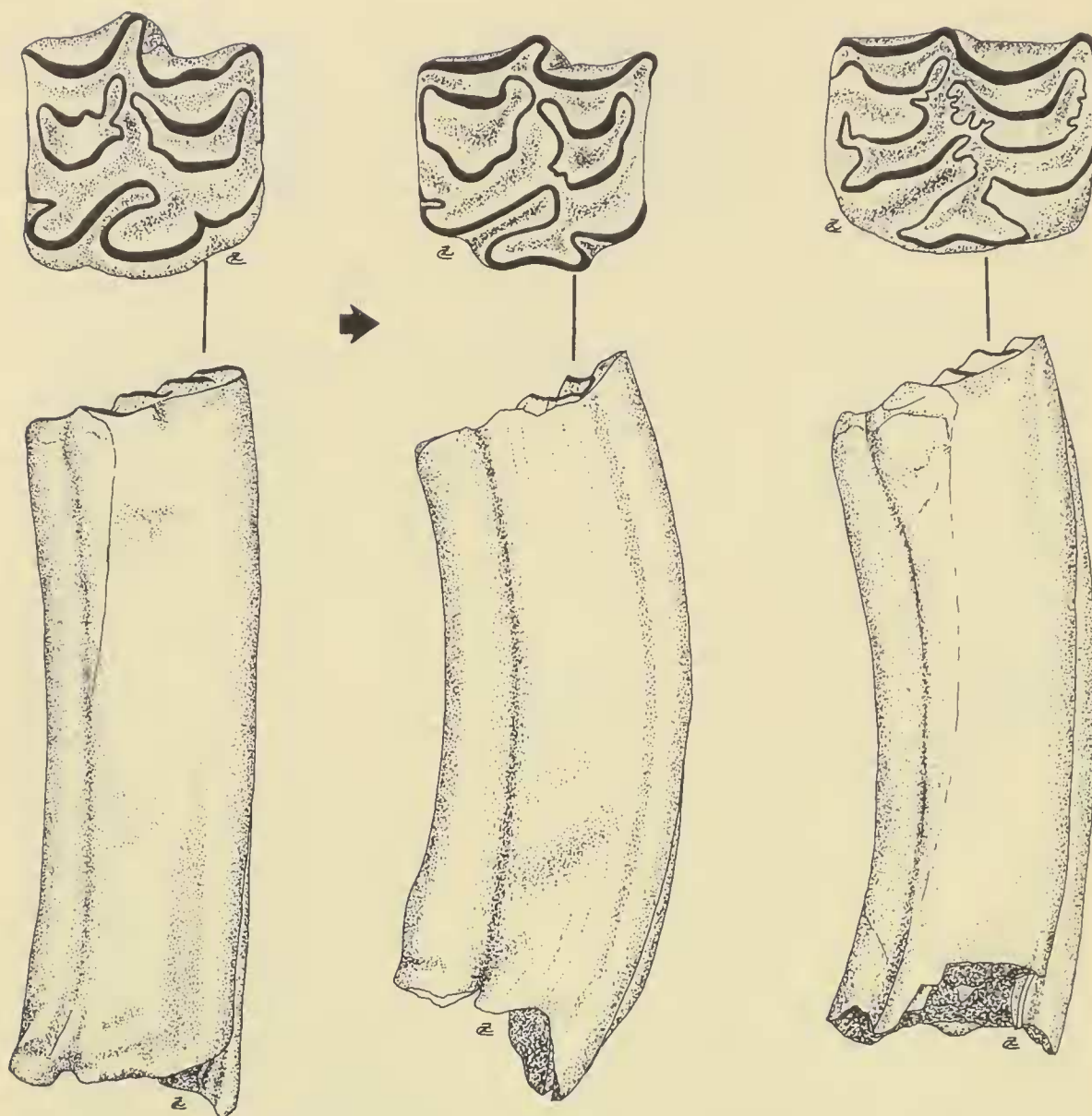


FIG. 5.—Variation in shape of protocone of upper teeth in *Astrohippus albidens* from the late Hemphillian Ocote local fauna of México. Arrow indicates anterior. Left, primitive type (MWSU 11424-98, first molar) with short isthmus, oval protocone, and protoconal body lying entirely posterior to anterior border of isthmus (a rare condition at Ocote, late Hemphillian, more common at the Coffee Ranch, mid-Hemphillian). Middle, grooved, flattened protocone with part of the body extending anterior to the isthmus (MWSU 11424-838, second molar, the common type at Ocote). Right, elongated isthmus and flattened protoconal body with much of the body lying anterior to the isthmus (MWSU 11424-638, second molar, not uncommon at Ocote and the dominant type in *Equus* and *Asinus*).

the anterior wall of the protocone or bends forward at an angle to form a pointed anterior tip. The lingual wall may become grooved, but usually not deeply so. Little of the protoconal body lies anterior to the isthmus.

In the contemporary *Astrohippus albidens*, similar changes occur. The protoconal isthmus remains short but the body juts forward to form a small rounded or angular tip anterior to the

isthmus. The lingual wall becomes grooved, sometimes strongly so, to form a wooden-shoe shape. Occasional individuals have elongated, flattened protocones like the advanced condition seen in *Equus* and *Asinus*.

In the unworn upper molars, of hypsodont horses, the cusps form rounded eminences at the tops of the teeth. The hypocone is distinct at the postero-lingual corner of the tooth. The somewhat triangular depression labial to it is the top of the hypoconal groove. Variation in development of the hypoconal groove is seen in the large series of teeth of *Astrohippus albidens* from the Ocote local fauna.

There are 24 teeth, upper P3-M2, of *Astrohippus albidens* that have the very crests of the teeth unworn or only slightly worn, but observation through the open bases of the teeth shows that internally the enamel columns had closed. (Second premolars and third molars are not included, but these also possess hypoconal grooves—Fig. 6.) These 24 teeth show no external trace of a hypoconal groove other than a shallow, liplike downfolding of the enamel that descends only a few millimeters. The depressed area behind the downfolding is invariably filled with thick cementum.

A typical hypoconal groove develops when the enamel of this depressed area folds inward at the edges, with the fold descending along the posterior face of the tooth, narrowing as it descends, to terminate somewhere above the root. In *Astrohippus albidens*, conditions of preservation at Ocote were such that the cementum that once covered the teeth is mostly eroded away, leaving irregular flakes and bits adhering to the enamel except along the length of the hypoconal groove. As the hypoconal groove formed in the growing tooth, cementum filled the groove to become locked by the infolded enamel edges. The height of the hypoconal groove internally is determined externally by the height of the band of cementum adhering to the posterior face of the tooth.

In many instances, the edges of a hypoconal groove fold completely around and fuse, enveloping a cementum-filled enamel column beneath the enamel of the tooth. This tube, a hypoconal fossette, occurs in both *Equus* and *Asinus*, usually only in the upper third of the crown. *Astrohippus* teeth that are fully grown but not worn and show no external hypoconal groove, such as the 24 teeth mentioned above, cannot be assumed to lack the groove. A hypoconal fossette, not visible externally, probably is present beneath the enamel in a good proportion of them.

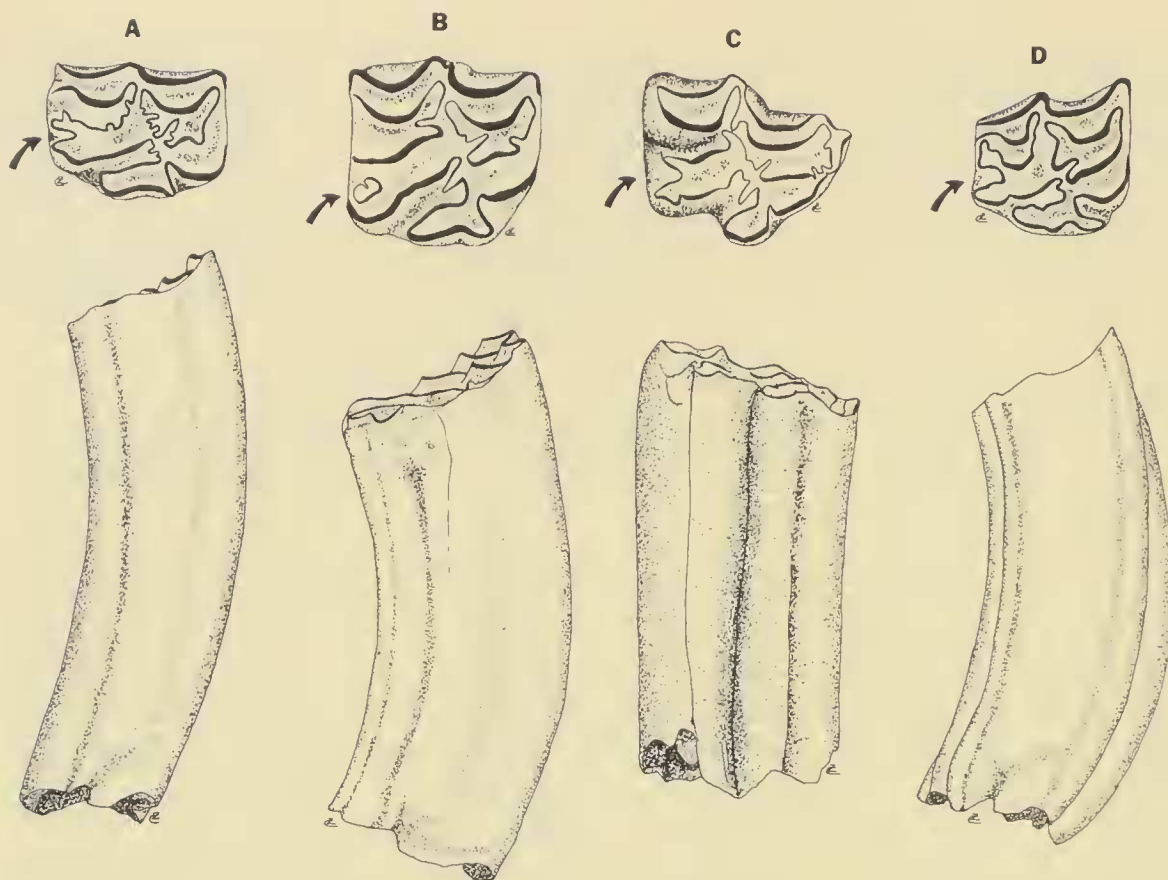


FIG. 6.—Variation in hypoconal groove (arrows) in *Astrohippus albidens*, Ocote local fauna, late Hemphillian, México: A, groove typical of upper P3-M2; B, hypoconal fossette (groove enclosed by outer tooth enamel); C, groove in second premolar; D, groove in third molar.

Dalquest and Mooser (1980) arbitrarily chose *Astrohippus* teeth more than 40 millimeters in minimum crown height in assessing the hypoconal groove in *Astrohippus albidens*. At that height, approximately half of 176 teeth possessed hypoconal grooves: 90 had no grooves, 45 had distinct grooves, whereas 41 had hypoconal fossettes. At a greater minimum height, 45 millimeters for example, the proportion of teeth with hypoconal grooves would have been greater. The groove rarely descended to less than 35 millimeters from the tooth base.

Astrohippus ansae is uncommon at the mid-Hemphillian Coffee Ranch Quarry of Texas. The teeth are more primitive than those of *A. albidens*, averaging shorter-crowned and more curved. Nevertheless, the hypoconal groove seems to occur in these teeth in proportions equal to the Ocote population, descending as deeply on the crown.

Lower molars of *Dinohippus interpolatus* typically have broad, deep ectoflexids that are often square-ended. Sometimes the ectoflexid almost passes through the metaconid-metastylid column to meet the base of the linguaflexid. Teeth from Ocote do

not differ appreciably from the older Coffee Ranch teeth in the nature of the ectoflexid.

Similarly, the ectoflexid seems not to differ in middle and late populations of *Astrohippus*. The fold is broad, sometimes with parallel and sometimes with gently converging sides. The rounded tip does not reach as far lingually as the floors of the preflexid and postflexid.

Dinohippus and *Astrohippus* differ markedly in the shape of the lingualflexid. The shape of this fold is determined by the shape of the protoconid and metaconid, presence or absence of curve of the inner walls of these cusps, and the amount of elongation of the labial apex of the lingualflexid. The metaconid-metastylid column is somewhat asymmetrical because the metaconid is almost always larger than the metastylid, but in molars (not always in premolars) the tips of ectoflexids and lingualflexids are opposed.

In mid-Hemphillian *Dinohippus interpolatus*, metaconid and metastylid are smoothly rounded, comparatively small, and somewhat oriented in the anteroposterior direction. The inner walls of the metaconid and metastylid tend to be convex, forming a rather narrow V-shaped lingualflexid. However, in some instances the ectoflexid approaches the apex of the lingualflexid so closely that the lingualflexid apex is stretched laterally, forming a flat-bottomed "V" or trapezoidal shape.

Dinohippus ocotensis lingualflexids differ little from those of *D. interpolatus*. Metaconids and metastylids appear to average larger and the trapezoidal lingualflexid, clearly a modification of the V-shape, may be more common.

In *Astrohippus ansae*, the metaconid and metastylid are less rounded and drawn out laterally, resembling not a double knot or bow but a pair of rabbit ears. The short, broad ectoflexid does not enter the molar isthmus and the tips of ectoflexid and lingualflexid are widely separated. The inner slopes of the metaconid and metastylid are usually straight, not convex, and the lingualflexid usually has a broad, shallow V-shape.

The lingualflexids of *Astrohippus albidens* differ little from those of *A. ansae*. However, some individual teeth have rounded metaconids and metastylids and some specimens have drawn out metastylids, appearing pinched at the tip, as in *Equus* and *Asinus*.

BLANCAN CABALLOID HORSES

By the beginning of the Blancan Land Mammal Age, *ca.* four million years BP (Lindsay *et al.*, 1980), the tridactyl hipparions were reduced to the single genus *Nannippus* Matthew. Caballoid horses included the modern genera *Equus* and *Asinus*. Evolution of the caballoid horses from mid-Hemphillian through the Blancan ages seems characterized by gradual, parallel change.

Blancan *Equus* are known from many local faunas, usually from lower jaws and teeth, but skeletons and skulls have been discovered, especially in Idaho. Blancan *Equus* have sometimes been placed in the separate genus, *Plesippus* Matthew, but Skinner *et al.* (1972) found all nominal species so similar that they could be placed in a single species, *Equus simplicidens*. This zebra was thought to be so closely related to the African zebra, *Equus grevyi* Oustalet, that both should be placed within the subgenus *Dolichohippus* Heller. Whether Blancan zebras should be placed in a separate subgenus and how many species are valid remains to be determined.

Equus simplicidens shows minor advances over late Hemphillian *Dinohippus*: protocones tend to be short, broadly oval to triangular; the hypoconal groove ends well above the base of the tooth enamel; ectoflexids are like those of *Dinohippus*; metaconids are rounded, the pinched shape rarely seen; linguaeflexids are V-shaped as in *Dinohippus*, but the elongated trapezoidal linguaeflexid, uncommon in *Dinohippus*, is found in most lower molars of *Equus simplicidens*. Facial fossae are still present in *E. simplicidens*.

The Blancan ass, *Asinus cumminsii*, was named from the Blanco local fauna of Texas by Cope (1893), who figured the lectotype upper molar. It, and all other reported upper teeth of *Asinus cumminsii*, are much worn and all lack a hypoconal groove (Dalquest, 1975). In upper teeth of *Equus simplicidens*, the hypoconal groove ends 15-20 millimeters above the base. In Blancan asses it was lost 25-30 millimeters above the base, an *Astrohippus* character. In Pleistocene and Recent horses, the groove extends almost to the base of the tooth.

Asinus cumminsii was based on three isolated upper teeth. No associated upper and lower dentitions have been found. However, there are three associated lower teeth from the Blanco—probably p4, m1, and m2. These teeth are characteristic of an ass: small size, ectoflexid not penetrating the molar isthmus, and sharply V-shaped linguaeflexids. Doubtless these are lower teeth of *Asinus cumminsii*.

Asinus cumminsii seems to have been rare. Lower jaws have been reported from Blancan deposits in Kansas by Hibbard (1944), by Strain (1966) from Texas, and isolated lower teeth from Texas by Akersten (1970). Johnston and Savage (1951) noted "*Astrohippus* or diminutive *Equus*" from Cita Canyon, Texas, that might be *Asinus cumminsii*.

The lower molars of *Asinus cumminsii* share the following differences from late Hemphillian *Astrohippus*: slightly larger size, rounder metaconids and metastylids, and linguaflexids narrowly V-shaped. These are characteristic of asses derived from *Astrohippus*. The characters are found in some specimens of late Hemphillian *Astrohippus*.

PLEISTOCENE HORSES

Horse evolution in the Hemphillian and Blancan ages was gradual, accelerating probably in the latest Blancan and early Pleistocene, providing an example of punctuated evolution (Eldredge and Gould, 1972). From one kind of Blancan zebra (*Equus simplicidens*), and one Blancan ass (*Asinus cumminsii*), each perhaps with a few closely related species, suddenly developed the variety of Pleistocene horses that has been the despair of paleontologists. The number of species names applied to these horses, taxonomically valid but often biologically indeterminate, has made the situation worse. Nevertheless, some simplification is possible.

Unlike the Old World, American horses with zebrine dentitions, descended from *Equus simplicidens*, are few in species and rare. Among the many lower jaws and isolated lower molars of horses in the Gilliland local fauna of Texas (Irvington Land Mammal Age), is a lower jaw fragment that is almost unique (Hibbard and Dalquest, 1966). It is the only lower jaw of a medium-sized horse in a collection that consists of more than 90 percent fossils of the large "*Equus*" *scotti* Gidley. The teeth were recognized as *Equus*-like rather than ass-like, although the value of the ectoflexid as an *Equus* character was not recognized at that time. Since then, two additional teeth have been recovered. The molars have deep, *Dinohippus*-type ectoflexids but have broad, U-shaped linguaflexids.

The dentition of *Equus parastylidens* Mooser, early Rancholabrean Land Mammal Age, of Aguascalientes, México, is distinctly zebrine. The ectoflexids are of the *Dinohippus*-type, linguaflexids are V-shaped, and parastylids are present on the lower molars. In dental characters, *E. parastylidens* is indistinguishable from the

African lowland zebra, *Equus burchelli* (Gray). Only two lower jaws are known but the species is distinctive. Mooser and Dalquest (1975) proposed that this species be placed in a separate subgenus, *Parastilidequus*, but Forstén (1986b) objected to this and I now concur. Parastylids (protostylids of European authors) are apparently common in a number of Old World horses (Eisenmann, 1976), and may be a valuable species character. The character is derived, as parastylids do not occur in *Dinohippus* or *Equus simplicidens*.

Another group that may be separated from the American Pleistocene horses is the hemiones (stilt-legged horses, the living onagers). The long, slender metapodials of this group are especially distinctive. Lower dentitions associated with or confidently referred to as hemiones show *Astrohippus*-type ectoflexids and V-shaped linguaflexids. Species include the small *Asinus francisci* (Hay), the even smaller *Asinus tau* (Owen), and the medium-sized *Asinus calobatus* (Troxell). "*Onager*" *altidens* (Quinn) may be an ass or an onager but the name is a homonym of *Equus altidens* Reichenau.

The most common American Pleistocene horses are not zebras, asses, or hemiones but species with *Astrohippus*-type ectoflexids, U-shaped linguaflexids, and comparatively short, stout limb bones of normal proportions. Fragmentary upper and lower jaws, teeth, and limb bones are the fossils workers usually find in American Pleistocene deposits. In the absence of an authoritative revision of the American Equidae, individual workers have adopted arbitrary and variable, but workable, standards for identification of species, based largely on size.

In the Great Plains region, teeth and metapodials of large-sized horses may be referred to "*Equus*" *giganteus* Gidley. Large specimens with uniquely large incisors are referred to "*Equus*" *scotti* (large horses with incisors of normal size should not be termed "*E.*" *scotti*); fossils of medium size often are referred to "*Equus*" *niobrarensis* Hay (use of "*E.*" *niobrarensis* for specimens of medium size is inconsistent with priority; "*E.*" *excelsus* Leidy, based on a maxillary from Nebraska, would be a better choice); and small fossils are assigned to "*E.*" *conversidens* Owen. Large horses from east of the Great Plains are sometimes referred to "*E.*" *complicatus* Leidy. "*Equus*" *occidentalis* Leidy, has the *Astrohippus*-type ectoflexid, U-shaped linguaflexids, but primitive, short, sometimes triangular protocones in the upper molars, resembling those found in *E. simplicidens*.

Numerous advances in the understanding of Old World horses have been made in recent years, especially through the works of Azzaroli (Italy), Eisenmann (France), Forstén (Finland), Gromova (USSR), and others (for references see Forstén, 1986*b*). The model for Eurasian horse evolution is summarized mostly from Azzaroli (1982) and Forstén (1986*b*) as follows. *Equus simplicidens*, or a related species, reached the Old World in the Villafranchian (Blancan) Land Mammal Age (Eisenmann, 1978). As in America, rapid radiation occurred. Unlike America, where zebrine horses were scanty in the Pleistocene, zebrines dominated the Villafranchian and early Pleistocene fauna in Eurasia. Caballine horses, derived from zebrine ancestors, became common in the later Pleistocene. Hemiones and asinines appear to have been less important and seem to be close to American taxa (Skinner *et al.*, 1972).

Perhaps oversimplifying, Old World zebrine horses have *Dinohippus*-type ectoflexids, but V-shaped linguaflexids in the lower molars. Caballine horses have *Astrohippus*-type ectoflexids and U-shaped linguaflexids, except that *Equus caballus* (domestic horse and wild, Przewalski's horse) may have either *Dinohippus* or *Astrohippus*-type ectoflexids. (The proper use of *E. caballus*, *E. przewalski* Poljakoff, or *E. ferus* Boddaert for the wild horse seems controversial—see Azzaroli, 1984.) Asinines and hemiones have *Astrohippus*-type ectoflexids and V-shaped linguaflexids.

In contrast with the Pleistocene horse fauna of America, zebrine horses were important in Eurasia and the evolutionary transition from zebrine to caballine horses is documented in the fossil record. American Pleistocene horses appear to be either zebrine or asinine, with no transitional or intermediate caballines indicated. It is usually assumed that caballine horses did not occur in America (but see Savage, 1951) and that the U-shaped linguaflexid, so common in American species, is simply a variable character.

The evolution of Old World caballine horses, with short, *Astrohippus*-type ectoflexids, from zebrine ancestors that had V-shaped ectoflexids is another example of convergent evolution in the Equidae. In the Pleistocene asses, the short ectoflexid is a primitive character that was inherited from *Astrohippus* through *Asinus cummingsii*. In Eurasian caballines, it is a progressive character, evolved from a zebrine ancestor millions of years later. It might pass unrecognized as a new development were it not accompanied by a second derived character, the U-shaped linguaflexid.

The viewpoints of European and American paleontologists have been brought into direct opposition. Harrington and Clulow (1973) described and figured the holotype skull and lower jaws of the Pleistocene horse, *Equus lambei* Hay, from Gold Run Creek, Yukon Territory, Canada. The lower molars have *Astrohippus*-type ectoflexids and broadly U-shaped linguaflexids, and Harrington and Clulow (1973), in keeping with American practice, referred the specimen to the subgenus *Asinus*. Forstén (1986a), utilizing the same characters but from the European viewpoint, considered the specimen to be of a caballine horse closely related to *Equus przewalski* (also see Eisenmann, 1985). Had the skull of *E. lambei* been discovered in Eurasia it would have been considered by European biologists to be a caballine horse. If it had come instead from the Great Plains region, for example, it would have been considered, as by Harrington and Clulow, an ass. Because it was obtained in a part of Beringia, where faunal exchange between America and Siberia is known to have taken place, its identification becomes subject to disagreement. The dental characters of *Equus lambei* (short ectoflexid but broad U-shaped linguaflexid) are typical of many American Pleistocene horses. If *E. lambei* is judged to be a caballine horse, so also must be many of the American Pleistocene horses.

The transition from zebrine to caballine horses must have taken place in Eurasia for it is not indicated in America, unless the horse (mentioned previously) of the Gilliland local fauna be considered an example. This species has zebrine ectoflexids but somewhat U-shaped linguaflexids, not unlike *Equus caballus*, and may be an emigrant from Eurasia. A Pleistocene interchange between America and Siberia might have been a simple matter for horses. They are large, powerful animals, capable of traveling many kilometers in a single day. Presumably Pleistocene horses, like modern species, were social and occurred in herds, such that any herd might be a nucleus for faunal exchange. They would have found the grasslands of Beringia continuous stretches of suitable habitat. It is conceivable that the nonzebrine, nonasinine horses of the American Pleistocene were descendent from Old World immigrants that had evolved the *Astrohippus*-type ectoflexid and U-shaped linguaflexid in the Old World.

Forstén (1986b) considered the shape of the linguaflexid more important than the ectoflexid in identification of horses. This may be true in the Old World but its utility has not been proven in America. McGrew (1944) noted that Blancan zebrine horses

always had V-shaped linguaflexids and, with the reservation that some individuals have the base elongated to a trapezoidal shape, this holds true. It is true also that asses and hemiones always seem to have V-shaped linguaflexids. The bulk of American Pleistocene horses are not zebrines, hemiones, or asses (at least not in the sense of having sharply V-shaped linguaflexids). However, American workers usually have considered the shape of the linguaflexid in most Pleistocene horses too variable to be of value, even at the species level.

The largest collection of Pleistocene horse fossils at hand is from the Cedazo local fauna of Aguascalientes, México, early Rancholabrean age (Mooser and Dalquest, 1975). From more than 100 lower jaws, jaw fragments, and sets of associated teeth, 54 specimens were selected that had the permanent m1 and m2 along with p4, m3, or both, permitting positive identification of molars. Aged specimens were rejected as were young individuals that did not have the m3 worn flat (young horses have elongated tops of the tooth crowns and the linguaflexids are drawn out and shallow). The specimens included at least seven species.

Identification of the linguaflexids as V-shaped or U-shaped was not easy, and required a value judgment. Extreme conditions are readily recognized as deeply U-shaped, with rounded apex of the linguaflexid, or sharply V-shaped, but there are many intermediates. Most linguaflexids could be assigned as U-shaped or V-shaped with little difficulty but a number had to be arbitrarily assigned. Three specimens had the m1 linguaflexid of a different shape than that of the m2; 18 had the linguaflexids of both m1 and m2 V-shaped, and 33 had the linguaflexids of both m1 and m2 U-shaped.

Lower molars of the zebra, *Equus parastylidens*, had V-shaped linguaflexids, as was expected, and the tiny *Asinus tau* had narrow, sharply defined V-shaped linguaflexids, also as expected. Of the remainder, 17 (35 percent) had V-shaped linguaflexids and should be either asses or hemiones, and 32 (65 percent) with U-shaped linguaflexids should be caballines.

This simple experiment does not confirm the value of the linguaflexid shape in separating asses and hemiones from the nonasinine American horses but it is suggestive. If U-shaped linguaflexids are consistent in collections of single species of confidently identified lower jaws from single or adjacent sites ("*Equus*" *scotti* or "*E.*" *occidentalis*, for example), the value of the linguaflexid will be better established. This will strengthen

the concept that caballine horses were common in the American Pleistocene and cause American workers to rethink current idea.

OTHER CHARACTERS

South American horses sometimes have been placed in the subgenus *Amerhippus* Hoffstetter, on the basis of absence of infundibulae in the lower incisors. Eisenmann (1979) has studied the incisors of numerous species of horses and finds the infundibulae variable, "the result of a parallel evolution expressing a common evolutionary tendency rather than a synapomorphy." Absence of infundibulae, like the presence of parastylids in lower molars, is of value at the species level.

Skulls of Pleistocene horses should provide important data on classification. However, cladistic treatment will provide little of value until variation due to age and sex as well as individual variation are taken into account. Detailed statistical treatment of such variation should be possible with the 130 skulls of *Equus simplicidens* (*shoshonensis*?) in the U.S. National Museum (Gazin, 1936), the skulls of "*E.*" *occidentalis* from the Rancho la Brea, and the smaller but still probably important series of skulls of "*E.*" *scotti* in the American Museum of Natural History and elsewhere.

SUMMARY

It is postulated that during the middle and late Hemphillian Land Mammal Age, *Astrohippus* and *Dinohippus* followed gradual, parallel, but separate evolutionary patterns, with the two lineages always recognizable by the nature of the ectoflexid of the lower molars. By the Blancan Land Mammal Age the large *Dinohippus* had reached the *Equus* morphological level and the small *Astrohippus* the *Asinus* level, both differing slightly from their latest Hemphillian ancestors. Little evolutionary change is apparent in the Blancan: *Equus* was represented by the large zebra, *E. simplicidens* and perhaps a few closely similar species, and *Asinus* by the small *A. cummingsii*.

At the end of the Blancan and in the earliest Pleistocene, rapid radiation occurred in both the *Equus* and *Asinus* lineages, an example of punctuated evolution. In America, the zebrine horses became rare and seem to have vanished by the mid-Rancholabrean Land Mammal Age. *Equus simplicidens* made its way from America to Eurasia in the later Blancan, giving rise to the Old World (including African) zebras. In the Pleistocene, from zebrine

ancestors, evolved the caballine horses, *Equus caballus*, *E. przewalski*, and related species. The caballine horses evolved, as a derived character, the short, *Astrohippus*-type of ectoflexid, whereas the zebras retained the primitive, for them, *Dinohippus*-type ectoflexid. The caballine horses also developed, as a derived character, U-shaped linguaflexids in the lower molars. Both zebrine and caballine horses were medium to large in size.

The *Asinus* lineage, descendent from *Asinus cumminsii*, remained more conservative, at least in dental characters. The short, *Astrohippus*-type ectoflexid was retained (primitive in this lineage) as were V-shaped linguaflexids in the lower molars. The asses proper retained comparatively short limbs but the hemiones evolved slender, stilt legs. Species were mostly small but *Asinus calobatus* reached medium size. Both asses and hemiones reached the Old World and existed there to Recent times.

The change from zebras to caballine horses is not documented in America but European workers suggest that caballines emigrated from Asia to America in the Irvingtonian Land Mammal Age, giving rise to the common American Pleistocene horses with short ectoflexids and U-shaped linguaflexids. This thesis seems logical but remains to be proven.

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